DETERMINANTS OF WITHIN-PATCH MICRODISTRIBUTION AND MOVEMENTS OF ENDANGERED BUTTERFLY *COENONYMPHA OEDIPPUS* (FABRICIUS, 1787) (NYMPHALIDAE: SATYRINAE)

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Abstract

The within-patch microdistribution and movements of adults of the critically endangered butterfly, *Coenonympha oedippus*, were studied using mark-recapture data from an isolated patch network, which consisted of 8 patches in central Slovenia. The impact of patch characteristics on both parameters was analyzed. Males fly longer distances and spend more time flying than females. The distances and seasonal pattern of male movements were dependent on the patch size, and on the microdistribution and density of freshly emerged (receptive) females. The spatial and temporal pattern of female microdistribution was influenced by vegetation height, the homogeneity of host plant stands and the shading of the ground and/or the lowest parts of herb layer. In the case of near continuous distribution of host plants within a patch, the structure of herb vegetation appears to be the major determinant of adult microdistribution. It affects the dynamics of butterfly emergence and the selection of oviposition sites. The per cent cover of the nectar plant, *Potentilla erecta,* does not play an important role in butterfly microdistribution.

Key words: Mark–release–recapture, *Coenonympha oedippus*, microdistribution of adults, within-patch movements, vegetation structure, Ljubljansko barje.

Izvleček

V izoliranem omrežju osmih habitatnih krp v osrednji Sloveniji smo z metodo markiranja, izpusta in ponovnega ulova raziskovali prostorsko razporeditev in gibanja imagov kritično ogrožene vrste *Coenonympha oedippus* v habitatni krpi in vpliv značilnosti krpe na oba proučevana parametra. Samci preletavajo daljše razdalje in v dnevni aktivnosti več časa porabijo za let kot samice. Preletne razdalje in vzorci preletavanja samcev v sezoni so odvisni od velikosti krpe ter prostorske razporeditve in populacijske gostote sveže izleglih (receptivnih) samic. Na prostorske in časovne vzorce disperzije samic vplivajo višina vegetacije, homogenost sestoja hranilnih rastlin gosenic in osončenost spodnje plasti zeliščne vegetacije. Če je razporeditev larvalnih hranilnih rastlin v krpi enakomerna in kontinuirana, je struktura zeliščne vegetacije najpomembnejši dejavnik, ki določa disperzijo imagov, saj vpliva na dinamiko izleganja iz bub in izbiro mest za ovipozicijo. Pokrovnost vrste *Potentilla erecta*, ki je hranilna rastlina odraslih osebkov, ne vpliva na razporeditev odraslih osebkov v krpi.

Ključne besede: markiranje–izpust–ponovni ulov, *Coenonympha oedippus*, disperzija imagov v krpi, preletene razdalje v krpi, struktura vegetacije, Ljubljansko barje.

INTRODUCTION

The distribution and density of butterflies within a habitat is dependent on spatial distribution and temporal variability of resources (Loertscher et al. 1995, Ide 2002) which predominantly include host plants (Fischer et al. 1999, Luoto et al. 2001, Matter et al. 2003, Krauss et al. 2005), nectar plants (Ravenscroft 1994, Loertscher et al. 1995, Brommer & Fred 1999, Matter & Roland 2002, Schneider et al. 2003, Auckland et al. 2004), mate-location sites (Brakefield 1982, Schwarzwälder et al. 1997), oviposition sites (Chew & Robbins 1989) and microclimate (Gutiérrez et al. 1999, Luoto et

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al. 2001, Dennis 2004). The knowledge of movements and behaviour of adults within a patch is important for understanding the stages of the transfer process at a larger scale, i.e. emigration, migration, immigration (Ims & Yoccoz 1997), and also gives valuable insight into the potential for seasonal changes in movement patterns (Auckland et al. 2004) in response to changing resource distribution (Ehrlich 1989). In the case of high population density of females, or high ambient temperatures and/or homogenous distribution of resources within a habitat, patrolling strategy is the most relevant male mate location behaviour (Wiklund 2003). The density of receptive females and the ability of a male to locate, approach and copulate with one of them are two chief determinants of male's probability of mating, which are variable in relation to the vegetation structure (Brakefield 1982). The vegetation cover may have a greater impact on oviposition success than vegetation height (e.g. Fleishman et al. 2002) since the high density and height of sward decrease the female ability of locating the suitable host plants and the probability of successful egg deposition. The herbaceous vegetation also determines larval habitat quality, thus host plant size and architecture of vegetation surrounding the host are more important factors influencing female oviposition decision than the host plant abundance (Anthes et al. 2003, Konvicka et al. 2003). The suitability of host plant on which newly-hatched larva will find itself is then a result of its mother's egg-laying behaviour. Response of larva to host quality may involve the migration from the plant on which it hatched, or is already feeding, to a new host. The necessity for larval migration could be the result of a change in plant quality or larval preference or unsuitability of a host due to oviposition mistake or failure in conspecific discrimination among plants by females (Singer 1989). Hence, the suitability of plants that grow in physical proximity to initial host and the structure of herb vegetation could be important determinants of successful larval migration and further development in butterfly species using herbs as host plants, and consequently of adults microdistribution within a habitat patch.

The palearctic False Ringlet butterfly *Coenonympha oedippus* (Fabricius, 1787) inhabits central and eastern Europe, southern Siberia, Mongolia, north-eastern China, Korea and Japan (Gorbunov 2001, Bozano 2002). It is one of the most threatened butterfly species in Europe (e.g.

Heath 1981, Balleto & Kudrna 1985, SBN 1987, Lafranchis 2004, Staub & Aistleitner 2006), listed by van Sway & Warren (1999) as one of the seven critically endangered species. It has experienced more than 80 % population declines across its European range in the last three decades (van Sway & Warren 1999) and has become extinct in Slovakia (Pastoralis & Reiprich 1995), Bulgaria (Abadijev 2001) and Switzerland (Staub & Aistleitner 2006), leading to its inclusion on Annex II of the Bern Convention and the Habitats Directive (92/43/EEC). Mostly isolated populations are still present in France (Lafranchis 2000), Liechtenstein (Staub & Aistleitner 2006), Austria (Aistleitner et al. 2006), Italy (Balleto et al. 2005), Slovenia (Čelik et al. 2005), Croatia (Kučinić et al. 1999), Hungary (Vozar et al. 2005), Poland (Buszko 2005), Russia (Gorbunov 2001), Ukraine and Belarus (Tshikolovets 2003). In Europe the species inhabits alkaline fens (*Caricion davallianae*), Purple Moorgrass meadows (*Molinion caeruleae*) and bogs, wet heathlands (*Ericion tetralicis*), sedge communities at marginal zones of swamps, mesophytic forest meadows (Lhonore 1996, Lhonore 1998, Lhonore & Lagarde 1999, Gorbunov 2001, Winiarska 2001, Čelik 2003, Staub & Aistleitner 2006), and dry grasslands in early successional stages (e.g. Hafner 1910, Sajovic 1910, Kolar 1919, 1929, Habeler 1972, Čelik 2003; in prep.). Very important habitats of the species in southwestern France are also firebreaks and open stands in plantations of native maritime pine (*Pinus pinaster*) with a high cover of *Molinia caerulea* s.str. in herb layer (van Halder et al. 2008).

The species *C. oedippus* was studied in the isolated patch network in central Slovenia, the only one in the country colonized by hygrophilous population of the species. The aims of the study were to (1) investigate the ecological requirements and daily activity of adults, (2) analyze the impact of patch characteristics (area, vegetation) on butterfly density and within-patch movements, and (3) identify resources, which determine within-patch microdistribution of butterflies.

2. MATERIALS AND METHODS

THE SPECIES

In Slovenia *C. oedippus* currently shows a disjunct distribution, being restricted to central (wider Ljubljansko barje) and southwestern part (Pri-

morska) (Čelik et al. 2005). In central Slovenia adults fly in one generation from early June until mid July on alkaline fens and extensive wet meadows with Purple moorgrass (*Molinion caeruleae*). In Primorska region the species inhabits first successional stages of abandoned, floristically poor, slightly overgrown submediterranean–illyrian dry grassland *Danthonio–Scorzoneretum villosae* (Čelik 2003). Previous studies have shown that (1) males emerge before females (protandry) (Drouet 1989, Čelik 2004); (2) male mate-locating behaviour is patrolling (Čelik 1997); (3) females mate two or three times (Lhonore 1998), the first copulation happens the day after the emergence of the female (Lhonore 1996); (4) adults feed very rarely (Čelik 1997, Lhonore 1998); (5) the nectar plants are species of *Cyperaceae* (but, we question this, because the floral nectaries are absent in this family), *Asteraceae*, *Fabaceae* (Lhonore 1996), *Lythrum salicaria*, *Frangula alnus*, *Mentha* sp., *Rubus* sp. (Lhonore 1998), *Potentilla erecta* (Čelik 2004), *Potentilla reptans*, *Inula salicina*, *Dianthus liburnicus*, *Gratiola officinalis* (Šašić, pers. comm.); (6) the host plants are *Molinia caerulea* s.str., *Carex flava*, *C. hostiana*, *C. panicea*, *C. flava* s. lat. x *hostiana*, *C. davalliana* (Čelik 1997, 2003, 2004), *Schoenus nigricans*, *Poa annua*, *P. palustris, P. pratensis* (Chretien 1886, Lhonore 1996, Lafranchis 2000), *Lolium* sp. (Tshikolovets 2003), *Pseudoarrhenatherum longifolium* (Dierks 2006), and *Eriophorum* spp. (Weidemann 1995); (7) larva pupates on food-plant (Čelik 1997); (8) species is sedentary (Čelik 1997, 2003, Lhonore & Lagarde 1999, Vozar et al. 2005). *Potentilla erecta* is the only observed nectar plant of *C. oedippus* on Ljubljansko barje.

Study area

The research was carried out within an isolated patch network in central Slovenia, on Ljubljansko barje (45º59' N, 14º26' E), at an elevation of 290 m. The central plain is exposed to regular flooding. The present appearance of the Ljubljansko barje plain is a mosaic of drainage ditches, corn fields, intensively cultivated and fertilised meadows, pastures, hedges, abandoned farmland, cart tracks and roads, extensively managed wet meadows, remains of raised bogs and alluvial forests, where only small patches of the former alkaline fens have been preserved.

Field methods

Mark–Release–Recapture (MRR) study
The MRR study was carried out during the entire flight-period of *C. oedippus*, weather permitting (cf. Pollard & Yates 1993), from 14 June to 14 July 1996 and from 12 June to 21 July 2001. In 1996 an intensive MRR study with 15 capture sessions was carried out in one of the largest habitat patch (patch No. 1) to investigate microhabitat preferences and within-patch distribution of butterflies. In May 2001 all suitable habitat patches for *C. oedippus* on the entire area of Ljubljansko barje were mapped and then checked for the presence of the imagoes in June of the same year. In 2001 on average eight capture sessions were performed in each occupied habitat patch. Within patches, standard transects were walked at each visit. Butterflies were netted and marked with an individual number on the underside of the left hind wing with a thin-point permanent pen (Stabilo-OHPen 841 S) and immediately released at the location of their capture. For each observation, the individual number, sex, co-ordinates of the capture location and time of the day were recorded. The co-ordinates were GPS measured.

Vegetation surveys
During the flight-period of *C. oedippus* the relevés on plots 10 ×10 m were performed in each habitat patch applying the standard Central-European phytosociological method (Braun-Blanquet 1964). The number of relevés in each patch was selected considering the patch size and heterogeneity. The relevés were stored and analysed in the FloVegSi database (Seliškar T. et al. 2003). According to floristic and structural variations the vegetation types were determined at the syntaxonomical range of association, subassociation or variant. In each relevé the mean height (in cm) of the herb vegetation was recorded with direct measurements.

Data analyses

Characteristics of habitat patches
GPS waypoints recording during the walk along the patch boundary were overlaid on digital aerial photographs (Ortophoto DOF050 1 : 5000; GURS) to calculate the patch area (AREA) using Arc Map 9.2 (ESRI 1999–2006). The study area of patch no. 1 researched in 1996 was smaller (2.6

ha) than in 2001 (3.7 ha) because the eastern part of patch was mown before the flight-period of *C. oedippus*. The height of herb layer (HEIGHT) in patch is defined as the ratio of the sum of mean heights and the number of relevés in patch. The per cent cover of known species' host plants (HOST) in patch was estimated as the median of per cent covers calculated for all patch relevés. In the same way the per cent cover of nectar plant, *Potentilla erecta* (NECTAR) was calculated. The per cent cover of plant species was derived from the Braun-Blanquet estimates as suggested by Tregubov (1957).

Microdistribution of adults

The handling of adults (capturing, marking) using MRR method may change their behaviour which could affect the survival of marked individuals or their probability of being recaptured (e.g. Morton 1989). Considering this fact, we used three methods to test the effect of handling on subsequent activity of adults in patch no. 1 in 1996 (in which microdistribution of butterflies was studied): (i) Manly's test for the marking effect (Manly 1971), (ii) the joint residence-catchability test (Tabashnik 1980) and (iii) capture probability from the best-fitting Jolly-Seber model using the POPAN module (Cooch & White 2008) in MARK, v. 5.1. (White 2008). The methods applied have shown that (1) marking did not affect the survival of adults (Čelik 1997) and (2) the capture probability was not sex specific (Čelik 1997, in prep.). These results indicate that possible gender-based behavioural differences in imagoes of *C. oedippus* do not bias the analyses of microdistribution of adults based on the number and density of their captures in the patch. The microdistribution of adults within a patch was then defined in two ways: as distribution of capture co-ordinates of (a) all captures, and (b) individuals captured for the first time (treated as freshly emerged according to intensive MRR study in 1996). According to the height of the herb vegetation, the area of patch no. 1 was divided in two parts: central (in the centre of patch) and marginal (on the east and on the west side of the central part). We examined whether the type of vegetation determined with the composition and structure of herb layer affects the microdistribution of the butterflies. The microdistribution of adults was analyzed as distribution of capture co-ordinates between both parts of patch, calculated separately for two sexes and for two periods of flight season, first

half (days 1 to 14) and the second half (days 15 to 31). The composition and the structure of herb layer was estimated with five parameters: the mean height (cm), the cover of nectar plant (%), the cover of known species' host plants (%), the homogeneity of host plant stand (index of homogeneity), and the shading of the ground and/or the lowest parts of herb layer (index of shading). Index of homogeneity (I_H) is defined as a quotient between the cover of H-herbs (%) and the cover of host plants, where the H-herbs include all plant species of herb layer except host plants. Index of shading (I_S) is defined as a quotient between the cover of S-herbs (%) and the sum of the cover of host plants and the cover of G-herbs (%), where cover(S-herbs) = cover(H-herbs) − cover(G-herbs), and G-herbs are species of the families *Poaceae*, *Cyperaceae* and *Juncaceae* (plant stature of these species does not shade the lower parts of herb layer) except host plants. Because the host plants were continuously distributed in the patch, the values of both indexes mean: I_H=0: the stand of host plants is homogeneous; 0< I_H <1: the stand of host plants is a fine mosaic where the cover of H-herbs is smaller than the cover of host plants; I_H≥1: the stand of host plants is a coarse mosaic where the cover of H-herbs is equal or greater than the cover of host plants; I_S=0: no shading; 0< I_S <0.5: moderate shading; 0.5≤ I_S <1: vast shading; I_S≥1: complete shading. Within the herb layer the sum of cover values of all plant species can exceed 100 % cover because of structural overlap of the constituent plants.

Density and within-patch distances of adults

In 1996 (when intensive MRR study was performed in patch no. 1) the density of adults was defined as (a) density of captures, and (b) density of individuals captured for the first time (i.e. density of marked population). For each sex it was calculated separately for two parts of patch (central, marginal) and for two periods of flight season (first and second half) as a ratio of the number of captures (no. of ind. captured for the first time) and the area of the part of patch.

In 2001 (when extensive MRR was performed in 8 patches) the density of adults was defined as density of marked population. It was calculated for each sex as quotient between the number of individuals marked in the patch and patch area.

Within-patch flight distance of an individual was calculated as straight line connecting two subsequent points of capture.

Statistical analyses

The non-parametric Spearman rank correlation coefficient (r_s) was used for analyzing the relationship between patch characteristics (area, vegetation height) and species variables (density, within-patch flight distances). For comparing the difference between the average of the two vegetation characteristics (per cent cover of host and nectar plants, vegetation height, I_H, I_S) and of within-patch distances moved by adults according to sex or time of flight season the non-parametric Mann-Whitney test was applied.

The spatial and temporal trends in distribution of adult captures within a patch during the flight season were analyzed with the chi-square tests for homogeneity and association. The Yates' correction for continuity (Fowler & Cohen 1992) was applied to each cell in 2 × 2 contingency table (test for association), and in the case of only two categories in test for homogeneous frequencies. In test for homogeneous distribution of number of captures (and individuals captured for the first time) between both parts of patch the expected frequencies were calculated considering the proportion of each part in the whole patch area.

All statistical analyses were performed using SPSS 13.0 (SPSS Inc., 1989–2004).

Nomenclature

The vascular plant nomenclature follows the Register of the Flora of Slovenia (Trpin & Vreš 1995), the Mala flora Slovenije (Martinčič et al. 2007) and Flora Europaea (Tutin et al. 1980); the vegetation type nomenclature follows the Süddeutsche Pflanzengesellschaften (Oberdorfer 1978, 1983) and Rastlinstvo Primorskega krasa in Slovenske Istre (Kaligarič 1997).

3. RESULTS

ECOLOGICAL REQUIREMENTS AND DAILY ACTIVITY OF BUTTERFLIES

Twenty-one patches of suitable habitat for *C. oedippus* were identified, eight of them were occupied in 2001 (patch No.1 was the same as in 1996), varying in size between 0.4 and 6.1 ha (Table 1). The vegetation in patches belonged to 14 variants of 4 communities: *Schoenetum nigricantis*, *Caricetum davallianae* (2 variants), *Molinietum caeruleae* (10 variants) and *Junco-Molinietum*.

Table 1: The area and the mean height of herb vegetation in habitat patches, and densities of marked populations of the species *Coenonympha oedippus* on Ljubljansko barje in 2001.

Patch	AREA (ha)	HEIGHT (cm)	Density of marked population (ha^{-1})	
			♂	♀
1	3.7	47	33	23
2	6.1	52	16	5
3	2.3	58	23	16
4	4.3	66	3	2
5	1.5	44	20	23
6	0.4	40	31	31
7	0.4	55	26	26
8	0.6	60	38	13

Among 1624 observations (males: 979, females: 645) of activities of adults recorded immediately prior to capture in 1996 and 2001, flying was observed 851 times (52 %), resting/basking 749 times (46 %), feeding 6 times (0.3 %), copulating 7 times (0.4 %), and ovipositing 4 times (0.2 %) (Fig. 1). The adults stay in the lower level of the grassland vegetation during resting, basking, feeding, copulating, ovipositing and also flying. In accordance with patrolling strategy males spend more time flying (71 % of their daily activities) than females (24 % of their daily activities). Strong wind greatly reduces the flight activity of butterflies in open habitat patches: adults predominantly quietly rest on the lower part of the plant stems. When butterflies soar, the flight is wind-assisted. In such patches adults are affected already by moderate wind gusts. Fe-
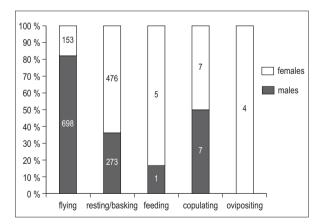

Figure 1: Daily activities of adults recorded immediately prior to capture in 1996 and 2001. The number in column represents the number of observations.

males feed on nectar more frequently than males (Fig. 1). All occasions of feeding were observed between 12.00 and 14.00 CEST. Copulations were not concentrated to a specific time of day: out of capture sessions the earliest and the latest copula were observed at 9.30 and 18.30 CEST, respectively. The longest observed copulation was still not terminated after 65 minutes. The reproductive habitat and feeding habitat of females are the same. Among 13 egg-depositions observed it was observed that (i) eggs are laid on *Carex hostiana* (6 eggs), *C. panicea* (2 eggs), *C. davalliana* (1 egg), *Molinia caerulea* s. str. (1 egg) and also on *Gratiola officinalis* (3 eggs) which is not confirmed as larval food plant; (ii) eggs are deposited singly, on the edge of the blade or on the grass stem (*M. caerulea* s. str.); oviposition height is about 5–15 cm (*C. davalliana*, *G. officinalis*) and 15–30 cm (*C. hostiana*, *C. panicea*, *M. caerulea* s. str.) above the ground. All ovipositions were observed between 11.30 and 16.30 CEST.

During the flight season of 2001 a total of 578 butterflies (males: 354, females: 224) were marked in eight patches with mean vegetation height ranging between 44 and 66 cm (Table 1). There was negative correlation between density of marked population and the vegetation height for both sexes, but it was significant only for female population (males: $r_s = -0.19$, P=NS; females: $r_s = -0.73$, $P<0.05$).

Herbaceous vegetation quality and butterfly microdistribution

On the basis of eight relevés performed in patch no. 1 in 1996 (five in central and three in marginal part of patch), three vegetation types were determined (Table 2). There was no difference in cover of host plants between both parts of patch (Mann–Whitney $z = -0.45$; P=NS). The nectar plant, *Potentilla erecta* flowered over the entire flight-period, its cover in the marginal part was not significantly greater than in the central part of patch (Mann–Whitney $z = -1.59$; P=NS). The herb vegetation of the central part was of lower height (Mann–Whitney $z = -2.38$; $P<0.05$), and the lower parts of herbal layer and the ground were less shady (Mann–Whitney $z = -1.95$; $P<0.05$, 1-tailed) than in marginal part of patch. The cover of S-herbs, which was significantly lower in central than in marginal part (Mann–Whitney $z = -2.24$; $P<0.05$), shows the predominance

of G-herbs among H-herbs in central part. The S-herbs to G-herbs ratio greater than 1 is the reason for significant positive correlation between I_H and I_S indexes of marginal part of patch ($r_s = 1.00$, $P<0.01$). Indexes of homogeneity show (Fig. 2) that the stands of host plants were more homogeneous in central than in marginal part of patch, but the difference was not significant (Mann–Whitney $z = -0.75$; P=NS).

Table 2: Composition and structure of herb vegetation, and the distribution of the number of captures and the number of individuals captured for the first time between central and marginal part of patch no. 1 in 1996. The vegetation parameters are shown as median values.

	Central part	Marginal part
Area (ha)	1.8	0.8
Vegetation type*	JM	JM
	MC ch	MC
Height of herb layer (cm)	25	50
Cover of nectar plant (%)	5.0	17.5
Cover of host plants (%)	42.6	37.7
Cover of H-herbs (%)	63.1	98.1
Cover of S-herbs (%)	10.6	43.4
Cover of G-herbs (%)	38.1	37.8
I_H	1.48	2.6
I_S	0.13	0.57

No. of captures (No. of ind. captured for the first time)

First half of flight season

♂	383 (185)	68 (42)
♀	96 (61)	17 (8)

Second half of flight season

♂	54 (30)	41 (29)
♀	157 (63)	67 (43)

*JM = *Junco-Molinietum*
*MC ch = *Moliniteum caeruleae* subass. *caricetosum hostianae* var. *Danthonia decumbens*
*MC = *Moliniteum caeruleae* var. *Cirsium oleraceum*
 FS = Flight season

percent of individuals captured for the first time was higher in the second half (males: 49 %, females: 41 %) than in the first half (males: 19 %, females: 12 %) of flight season. The densities of freshly emerged butterflies were higher in the central than in the marginal part in the first period, but inversely in the second one (Fig. 3b) for
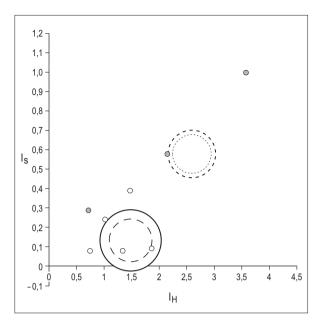
Figure 2: Structure of herb vegetation of central and marginal part of patch no. 1 in 1996 represented by indexes I_H and I_S, and density of adults in each part. Points indicate the relevés in central (○) and marginal (◉) part. Circles symbolize each part of patch where the size of circles represents the density of captures (—— central; - - - marginal) and of individuals captured for the first time (− − central; ······· marginal) respectively. Centroids of circles are median values of I_H and I_S for each part of patch.

During the flight season of 1996 a total of 461 butterflies (males: 286, females: 175) were marked in patch no. 1 (Table 2). The observed number (Table 2) and density of captures and individuals captured for the first time were higher in the central (density of captures, males: 240 ha^{-1}, females: 139 ha^{-1}; density of freshly emerged adults, males:119 ha^{-1}, females: 68 ha^{-1}) than in the marginal part of patch (density of captures, males: 135 ha^{-1}, females: 102 ha^{-1}; density of freshly emerged adults, males: 88 ha^{-1}, females: 63 ha^{-1}). The departure of observed frequencies from homogeneity between both parts of patch was significant for all population parameters except the number and density of freshly emerged females (Table 3).

In the first half of the flight season 83 % of all male captures were made, 85 % in central part and 15 % in marginal part of patch. The corresponding values for the second half of the flight season were 17 %, 57 % and 43 % respectively. The majority of captures of female population was in the second half of flight season when 66 % of female captures were done. A concentration of female captures also occurred in the central part of patch in both periods of flight season (first: 85 %, second: 70 %). In the marginal part of patch the

Table 3: Results of chi-square tests for analyzing the spatial and temporal changes in within-patch microdistribution of adults of the species *Coenonympha oedippus* during the flight period.

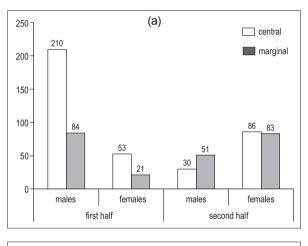| Parameter	Sex	Test for homogeneous frequencies	Test for association		
		part of patch (central vs. marginal)	*period of FS: part of patch*	*sex: part of patch*	
				1st half of FS	2nd half of FS
No. of captures	♂	$\chi^2_1 = 30.61$**	$\chi^2_1 = 36.83$**	$\chi^2_1 = 0.02$	$\chi^2_1 = 4.62$*
	♀	$\chi^2_1 = 5.55$*	$\chi^2_1 = 8.11$**		
No. of ind. captured for the 1st time	♂	$\chi^2_1 = 4.83$*	$\chi^2_1 = 22.06$**	$\chi^2_1 = 1.37$	$\chi^2_1 = 0.85$
	♀	$\chi^2_1 = 0.20$	$\chi^2_1 = 15.58$**		
Density of captures	♂	$\chi^2_1 = 29.94$**	$\chi^2_1 = 30.99$**	$\chi^2_1 = 0.01$	$\chi^2_1 = 4.13$*
	♀	$\chi^2_1 = 5.19$*	$\chi^2_1 = 8.27$**		
Density of ind. captured for the 1st time	♂	$\chi^2_1 = 4.63$*	$\chi^2_1 = 17.54$**	$\chi^2_1 = 1.48$	$\chi^2_1 = 0.52$
	♀	$\chi^2_1 = 0.15$	$\chi^2_1 = 15.06$**		

FS = Flight season
* Significant at P < 0.05
** Significant at P < 0.01

both sexes. The similar seasonal change in distribution was observed for density of male captures, but not for density of female captures which was higher in central than in marginal part of patch in both halves of the flight-period (Fig. 3a). The significant association between the period of flight season and part of patch for number and density of captures and individuals captured for the first time for both sexes (Table 3) means that observed frequencies of captures and of adults captured for the first time were higher than expected for the central part in the first half, and for the marginal part in the second half of the flight season.

In the first half of the flight season there was no association between the sex and the place of capture (central vs. marginal part), but it was observed in the second half for number and density of captures (Table 3). This significant asso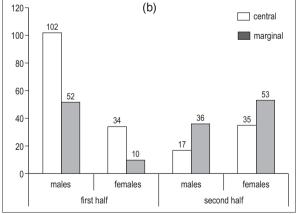ciation between variables (sex, part of patch) is the result of higher number of captures than expected for males in marginal part and for females in central part of patch. However, the microdistribution of freshly emerged adults was not significantly different between the sexes neither in the first half nor in the second half of the flight season (Table 3).

WITHIN-PATCH MOVEMENTS

The number of recaptures in eight patches in 2001 was 258 (males: 149, females: 109) for 169 individuals. The patch size affects the distances moved between successive capture events; in the large patches both sexes moved significantelly longer distances than in the small ones (males: $r_s = 0.44$, $P < 0.001$, females: $r_s = 0.30$, $P < 0.01$). No significant relationship between distance and time in successive captures was found for males ($r_s = -0.04$, $P = $NS) or females ($r_s = 0.18$, $P = $NS). Males and females moved a mean distance of 57 m and 40 m respectively (Fig. 4), the difference between sexes was significant (Mann–Whitney $z = -2.71$; $P < 0.01$). Maximum within-patch distances of males (399 m) and females (252 m) were 80 % and 50 % of maximum possible movement in the patch (= max. diameter of patch in the research area) respectively. Only 47 (18 %) of movements were greater than 100 m and 7 (3 %) further than 200 m.

In the first half of the 1996 flight season the distances made by males in patch no. 1 were significantly shorter (median = 50 m) than in the sec-
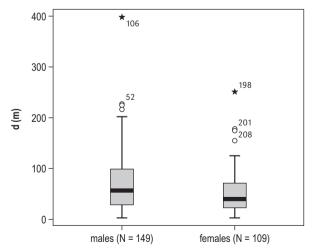

Figure 3: Distribution of densities of captures (a) and of individuals captured for the first time (b) between central and marginal part of patch no. 1 in 1996 according to the time of flight period.

Figure 4: Difference in within-patch distances (d) between males and females of *Coenonympha oedippus* on Ljubljansko barje in 2001.

ond half of flight season (median = 66 m) (Mann–Whitney z = −2.70; P<0.01). In the first period the majority of males patrolled across the central part of patch (Table 2) where the density of females was higher than in the marginal part (Fig. 3). The higher density of freshly emerged females in the marginal than in the central part in the second period (Fig. 3b) resulted in male movements between central and marginal part, and also between both marginal parts of the patch.

4. DISCUSSION

Factors affecting adult microdistribution

The distribution of number and density of captures and of adults captured for the first time within a patch no. 1 in 1996 showed that herb vegetation with mean height of 25 cm and moderate shading of its lower layers is more suitable for *C. oedippus* than the vegetation with similar floristic composition but of greater height and shading of herb layer in which S-herbs predominate (Table 2, Fig. 2). The host plant stands were not significantly more homogeneous in central than in marginal part of patch, but the index of homogeneity is still only an approximation because it is possible that not all actual host species were considered. According to species diversity of known larval food plants of *C. oedippus* (see Methods) we presume that some of observed G-herbs, especially short graminoids, are potential hosts of *C. oedippus*. Among them the species with high per cent cover, e.g. *Danthonia decumbens*, *Agrostis spp*. have great effect on the value of I_H if they are treated as larval food plants in calculations. This means that the cover of H-herbs decreases proportionally to the increase of host plants cover, and the I_H index higher than 1 decreases below 1 if the cover of potential hosts is higher than the value [cover(H-herbs) − cover(known hosts)]/2. The latter was the case in the central part but not in the marginal part. Consequently the difference in homogeneity of host plant stands between central and marginal part become greater still (i.e still more homogeneous in central than in marginal part) than was calculated on the basis of known larval food plants of *C. oedippus*. The mentioned treatment of G-herbs does not affect the value of I_S.

Our results show that the within-patch distribution of butterflies changed within the flight season: the adults were associated with central part of patch in the first half of flight season, and with marginal part in the second. This seasonal change in microdistribution may be caused by response to structure of herb vegetation. Namely, the number of freshly emerged adults was almost 5 times greater in central than in marginal part in the first period, and only 1.3 times greater in the second. Their density was 2 times greater in central than in marginal part in the first period, but in the second one the density of freshly emerged butterflies was 1.7 times greater in marginal than in central part of patch. This indicates that delays in butterfly emergence existed in the marginal part. Observed spatial variation in the adult time of emergence might be a consequence (i) of a delay in oviposition in marginal part according to central part in the previous year, or (ii) of the difference in length of larval development due to different developmental conditions related to microclimatic differences between both parts of the patch. The latter means that higher and more shaded herb vegetation extends larval development and consequently delays adult emergence. The more heterogeneous stand of host plants in marginal part of patch might also be the reason for longer larval development because it prolongs the time of searching for fresh host plant in vicinity of old food source, and consequently the time of larval migration from old host to fresh one.

The significant association between the male captures and marginal part and the female captures and central part of the patch in the second half of the flight period and absence of association between sex and part of patch for freshly emerged adults within the whole flight season indicates that (1) the microdistribution of males is affected by the microdistribution and density of freshly emerged (i.e. receptive) females, and (2) the microdistribution of fertilized females is influenced by spatial distribution of oviposition sites. Our results show that in the case of almost continuous distribution of host plants within a patch the suitability of these sites by ovipositing females is not determined by the cover of host plants but by the height and shading of herb vegetation and homogeneity of host plants stand (i.e. structure of herb layer). Only few observations of oviposition in the patch, with all observed egg laying in central part of the patch, also suggest that structure of herb layer influences the selection of oviposition sites that might correspond with the sites suitable for eggs and larval devel-

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opment. Consistent with this finding is also the negative correlation between density of marked population and vegetation height for both sexes in 2001 (Table 1). It was significant only for female population what might be a consequence of (i) a greater probability to rouse the sedentary female from lower than from higher herb vegetation, or (ii) of a sex-dependent effect of herb vegetation structure on success of survival to adulthood (e.g. Gibbs et al. 2004). The second possibility is less likely considering the density of freshly emerged adults within a patch in 1996. It was higher in central than in marginal part of patch for both sexes, but significantly only for males. Although the determinants of host plant suitability and of oviposition specificity need not be the same (Chew & Robbins 1989), it seems possible that in *C. oedippus* the oviposition preferences of females positively affect the larval survival.

No variation in the spatial and temporal availability of *Potentilla erecta* within a patch, and a low number of observations of adult feeding indicate that nectar source does not play a major role in determining adult microdistribution, consistent with the findings in the related species, *Coenonympha arcania* (Loertscher et al. 1995) and *C. glycerion* (Elligsen et al. 1997).

FACTORS AFFECTING WITHIN-PATCH MOVEMENTS

Our estimates of within-patch flight distances of *C. oedippus* are similar to the movements estimated in France (60–80 m) by Lhonore & Lagarde (1999), although direct comparisons are impossible because these authors did not report the size of their study patches. The dimensions of the study area is an important information for comparison of the movements of the same species studied at different spatial scales with MRR as the mean distance moved by butterfly increases with the size of the study area (Scott 1975, Schneider 2003, Schneider et al. 2003). Considering the daily activity and flight distances our results indicate that the females are more sedentary than the males. Females tend to hide in vegetation selecting ovipositing sites, laying eggs and feeding (the flowers of *P. erecta* are situated in the lower vegetation layer). More time spent in flight and longer distances moved by males are consistent with their patrolling strategy.

The within-patch movements of males showed

a pattern of seasonal changes with flight distances significantly longer in the second than in the first half of the flight-period. This could be clearly related to the seasonal change in microdistribution and density of freshly emerged females. In the case of low female density, the distances moved by males are greater, since the females are scattered and the likelihood of a male finding a receptive female is smaller. Mobility of males (especially as dispersal, not within-patch movements) inversely related to female density was also observed in other butterfly species, e.g. *Parnassius mnemosyne* (Välimäki & Itämies 2003), *Proclossiana eunomia* (Baguette et al. 1998), *Melitea cinxia* (Kuussaari et al. 1996), *Euphydryas editha* (Brussard et al. 1974, cited in Baguette et al. 1998, Gilbert & Singer 1973, cited in Kuussaari et al. 1996) and *E. chalcedona* (Brown & Ehrlich 1980).

5. CONCLUSIONS

Understanding the metapopulation dynamics of the endangered butterfly species is key to preserving its populations in a fragmented landscape. To gain unambiguous insight in the metapopulation dynamics of the species, the components of the transfer process (i.e. dispersal) in metapopulation (i.e. emigration, migration, immigration/colonization) must be understood (Ims & Yoccoz 1997). Dispersal of individuals is influenced by the environmental conditions (e.g. habitat quality, population density, local demografic structure) and the internal conditions (behavioural, morphological and physiological traits) (Ims & Hjermann 2001). Further, spatial and temporal variability of resources (e.g. host and nectar plants, sites for mate-location, oviposition and roosting, microclimate) as an important component of patch quality affects the butterfly movement patterns which are reflected in adult within-patch density and distribution. Therefore, the knowledge of within-patch behaviour of adults (e.g. understanding the environmental and internal cues used to emigrate and immigrate) may aid in explaining the population processes at a landscape scale. A much better understanding of determinants of the adults' within-patch distribution and movements also gives valuable information for conservation practice, e.g. implementation of an appropriate management for maintaining the most suitable floristic composition and vegetation structure in species' habitat. In central Slovenia, where *C.*

oedippus occupies patches with almost continuous distribution of host plants, the structure of herb vegetation appears to be the major determinant of adult within-patch distribution and density. It defines the seasonal changes in within-patch movement patterns of adults. Our results suggest that the movement patterns change during the flight season with the aim to maximize the probability of mating within a patch and to select the most suitable oviposition sites. The abundance of the nectar plant, *Potentilla erecta,* does not play an important role in seasonal changes of the adult within-patch distribution. These findings could form the groundwork for further studies on the mechanisms of species dispersal, and also for prior conservation actions focused on improvement the habitat quality for the species.

6. ACKNOWLEDGEMENTS

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